Functional Morphology of the Hind Tibial Spurs of the Cicada Killer (*Sphecius speciosus* Drury) (Hymenoptera: Sphecidae)

JOSEPH R. COELHO[1] AND KIMBERLY WIEDMAN

Department of Biological Sciences, Western Illinois University, 1 University Circle, Macomb, Illinois 61455, USA, (E-mail: JR-Coelho@wiu.edu)

Abstract.—The functional morphology of the hind tibial spurs in female cicada killers is examined in relation to digging. The spurs are controlled by a passive mechanical system using the corium; when the tarsus is flexed, the spurs are extended. The spurs resist extension, but not flexion. Videography demonstrated that the hind legs are used in burrow excavation to clear soil from the path of the wasp and that the position of the legs makes use of the spurs' resistance to extension. Spur function is not consistent with use during prey carriage, which should cause the spurs to lie flat. Enlarged spurs may have evolved from smaller structures used in grooming, and may reduce the energetic and temporal costs of burrowing.

The bodies of winged insects function in both aerial and terrestrial locomotion, which may present conflicting selection pressures on morphology. For example, flight performance may be improved by increasing the ratio of flight muscle mass to body mass (Marden 1987) at the expense of legs or associated muscles, but terrestrial locomotion would be adversely affected. Many insects also dig or burrow, which increases selection pressure for enhancement of the structures associated with the terrestrial mode. Although fossorial adaptation is relatively well understood in vertebrates (Hildebrand 1985), little of the function of specific adaptations of insects to fossorial life has been demonstrated. The Hymenoptera are generally excellent flyers, but many also dig burrows for nests. Therefore, they can be used to show how animals well adapted to flight handle the requirements of burrowing.

Various morphological modifications for fossorial life, such as foretarsal rakes, have been described in wasps (Bohart and Menke 1976), but their function has not been ascertained. An exception is provided by Gorb (1996), who examined pretarsal anatomy and function in a variety of insects. Fossorial species, such as the sphecid *Bembix rostrata* L., have a large unguitractor with well-developed microtrichia for the production of strong frictional forces with the substrate.

Cicada killers (*Sphecius speciosus* Drury) are the largest (by mass) North American sphecid (Horn 1976), and they are superb flyers. Relative to other Hymenoptera, they have a high ratio of flight muscle to body mass, resulting in a high degree of maneuverability. Females weigh nearly one gram in body mass, which allows them to carry cicadas (*Tibicen* spp.) heavier than themselves (Coelho 1997). Metabolic rate during hovering is high (Joos and Casey 1992), and body temperature during flight is elevated and nearly constant (J.R. Coelho, pers. obs.).

Female cicada killers also dig extensive burrows. A cicada killer may move up to 1000 times her body mass in dry soil while excavating her burrow (J.R. Coelho and

[1] To whom all correspondence should be addressed.

A.J. Ross, pers. obs.). The opening of the burrow is elevated in comparison to the rest of the burrow, and a large tumulus accumulates outside the entrance. The entrance tends to run at a 35–45° angle downward and then becomes more level (Evans 1966). The burrow branches into an average of 15.8 cells (Dambach and Good 1943), which are used to store paralyzed cicadas. The female lays one egg per cell. On average, cells may vary in diameter from 2 to 3 cm. Burrows vary in length from 30 cm to over 100 cm (Evans 1966). After provisioning the cell, the female cicada killer places a wall of dirt across the entrance. A variety of burrow architectures, as determined by excavation, are depicted by Riley (1892) and Evans (1966). After the main burrow is dug, the dirt from new cells is apparently used to plug old ones, although soil may be added to the tumulus as new cells are excavated.

The digging method uses a variety of body parts and behaviors. The cicada killer uses her mouthparts to loosen compact soil to begin excavating. She uses her fore legs to rapidly rake the dirt under and behind her body. Finally, she uses her hind legs to push the soil behind her as she backs out of the burrow (Frost 1942; Dambach and Good 1943; Evans and West Eberhard 1970). The latter behavior results in the formation of a prominent trough through the tumulus leading away from the burrow entrance (Dambach and Good 1943; Evans 1966).

Cicada killer females have a pair of enlarged spurs on the distal end of the hind tibia (see Evans [1966] for line drawings). Males have similar spurs which, by comparison, are much reduced (Dambach and Good 1943). While the presence of such spurs in bees and wasps has been a useful taxonomic tool (Eickwort and Fischer 1963), their functional significance has rarely been addressed (except by Cane [1979]). Some suggest that the spurs of female *S. speciosus* are used to support the cicada during prey carriage (Howes 1919;

Evans 1962), but our preliminary observations suggest that they are used to move soil during burrow excavation.

Hildebrand (1985) lists five requirements of a fossorial animal to loosen and move resistant material: a digging tool, the capacity to produce and transmit large forces, a transport mechanism for soil, passive resistance to various loads, and the ability to sustain activity. The cicada killer hind leg functions as part of the transport mechanism for soil, and we hypothesize that the spurs are morphological adaptations for that mechanism.

In this study we investigate the functional morphology of the hind tibial spurs in female cicada killers. Their mechanism of action is demonstrated, and their potential function relative to digging and prey carriage is examined.

MATERIALS AND METHODS

Origin of specimens.—Live cicada killers were obtained from local nesting aggregations in McDonough County, Illinois; and the legs of freshly killed individuals were used in all experiments. Unless otherwise mentioned, all data are reported as mean ± SEM (N).

Dissection.—We first investigated the mechanism for movement of the spurs. Under a dissecting microscope, a section of the exoskeleton was removed from the tibia near the tibiotarsal joint. Muscle tissue was examined for any connection to the spurs or to the corium, the unsclerotized conjunctival membrane which forms the distal end of the tibia and from which the spurs arise.

Mechanical linkage.—Five hind legs were obtained. When the tarsus of each was manually flexed, the spurs extended. Similarly, when the tarsus was extended, the spurs became flexed. The corium was severed by making an incision perpendicular to a line between the spurs and tarsus using a 30-ga syringe needle. The tarsus was flexed and extended again and the results were recorded.
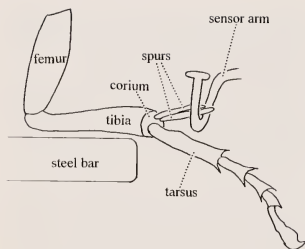
Fig. 1. Apparatus used to measure the force produced by the spurs. The spurs were extended by lowering the steel bar, to which the tibia was glued. The stationary force transducer measured the force exerted by the spurs during extension. To measure the force exerted during flexion, a similar set-up (not shown) was used, except that the sensor arm was placed above the spurs, and the steel bar was raised.

Having found that tarsal flexion causes spur extension, we measured the force generated by the spurs when they were extended in this manner. The tibia of an intact hind leg was glued to a steel bar. The tarsus was manually extended at different angles to the tibia, causing the spurs to extend. The spurs were oriented just below and perpendicular to the sensor arm of an optical force transducer (Narcosystems type A), which was calibrated with weights of known mass and connected to a physiograph (Narcosystems MK-III). The force exerted by the spurs was measured at tibia-to-tarsus angles of 180, 135, and 90° and recorded by the physiograph.

Force-displacement curves.—To determine the direction in which the spurs were capable of resisting force, the hind leg of a female wasp was removed and the tibia was glued to a steel bar with the spurs facing upward. To measure the effect of extension, spurs were placed on top of and perpendicular to the sensor arm of a force transducer connected to a physiograph (Fig. 1). An adjustable ringstand was calibrated so that fractions of a rota-

tion of the knurled adjustment ring could be used to move the bar known vertical distances. The angle between the spurs and the tibia was gradually increased by moving the bar downward in 0.07-mm increments. Measurements were taken until the ends of the spurs slipped off the force transducer. At this point the force was maximal, but the spurs had not yet broken. In this way, the resistant force exerted by the spurs when they were extended to various degrees was recorded by the physiograph.

To measure the effects of flexion, the spurs were extended manually, then placed just below and perpendicular to the axis of the force transducer. The bar was moved upward in 0.07-mm increments until the spurs laid flat against the tarsus. Hence, the force exerted by the spurs in resistance to varying degrees of flexion was recorded by the physiograph.

Videography.—Cicada killers were recorded with a Sony VHS-C videotape recorder while digging. Burrow entrances were plugged with a small amount of soil to induce digging in most cases, but spontaneous digging was also recorded. The tapes were replayed using slow motion to examine and describe aspects of digging behavior in detail.

RESULTS

Dissections.—Of the 10 hind legs dissected, no muscle or tendon attachment to the spurs or corium was found. The tarsus was traversed by a single tendon arising from the pretarsal muscles in the femur and tibia, an arrangement essentially identical to that described for honey bees (Snodgrass, 1956).

Mechanical linkage.—When the tarsus was manipulated and the corium was intact, tarsal flexion caused spur extension, and tarsal extension caused spur flexion in every case. The spurs always moved in one plane and resisted lateral movements. After the corium was severed, the spurs
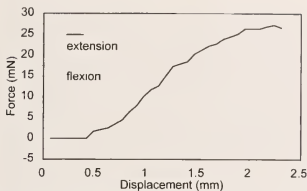
Fig. 2. Representative force-displacement curves for extension and flexion of the female cicada killer hind-tibial spurs.

no longer moved when the tarsus was manipulated.

When the tarsus was held at increasing angles relative to the tibia, the force produced by the extension of the spurs increased. When the tarsus was held at 180° to the tibia, no measurable force was detected. When the tarsus was held at 135°, an average force of $0.315 \pm 0.041(7)$ mN was detected. Finally, when the angle was decreased to 90°, an average force of $0.615 \pm 0.055(7)$ mN was produced.

Force-displacement curves.—Fig. 2 demonstrates that as the spurs are displaced, the force resisting extension increases linearly at first, then levels off near the maximum, while the force resisting flexion remains constant at zero until the spurs lie flat and touch the tarsus. Extension produced a maximum force of $21.68 \pm 2.13(8)$ mN, which is eight times greater than the maximum force resulting from flexion, $2.64 \pm 1.04(8)$ mN.

Video records.—Review of videotaped digging behavior in slow motion demonstrated how the female cicada killer uses the hind legs to move soil. A wasp broke off bits of soil from the burrow wall using the mandibles and threw them posteriorly under the body using rapid motions of the fore legs. She then backed out of the burrow, alternately thrusting her hind legs in arcs that began in a posterior direction and ended in a lateral direction, removing dirt from her path. Both front and rear

pairs of legs operated simultaneously, with fore leg raking being repeated during the recovery stroke of each hind leg. The tibiotarsal angle was near 90° at the beginning of the thrusting motion when the leg was cocked, then the angle increased as the leg was extended.

DISCUSSION

In dissections of the cicada killer hind tibia, no muscles or tendons were found leading to the spurs or corium. The spurs were extended with increasing force as the tarsus was flexed at increasing angles, suggesting that the spurs are not under direct muscular control, but that their degree of extension depends instead upon the angle of the tibiotarsal joint. When the corium was severed, the spurs no longer moved when the tarsus was manipulated. The corium, a flexible, unsclerotized conjunctival membrane, connects the tarsus and spurs. When the tarsus is flexed, it pulls on the lateral margin of the corium, which, in turn, pulls on the medial bases of the spurs, causing them to extend. When the corium is severed, this mechanical linkage is broken. Hence, the spurs are controlled by a passive mechanical system using the corium, as suggested by Cane (1979).

The spur extension system generates a very small force, less than 1 mN, which is sufficient to extend the spurs, but likely to be of little use otherwise. Hence, resistant forces determine what tasks can be accomplished by the spurs. The spurs produced a substantial resistant force to being extended outward, but not to being flexed inward (whereupon they simply fold flat against the tarsus). Only behaviors which flex the tibiotarsal joint, using the spurs' resistance to extension, are likely to effectively use the action of the spurs.

Hymenopteran hind tibial spurs are commonly used in grooming the contralateral hind leg (Farish 1972, Cane 1979), and we observed this behavior in captive cicada killers. The tibiotarsal joint is flexed

and brought under the body to the contralateral leg, where vertical motions up and down the second leg, held between the two spurs, occur (J.R. Coelho, pers. obs.). Known as L_3-L_3 grooming, this behavior occurs in all 15 superfamilies of bees and wasps tested by Farish (1972). Our data suggest that the downstroke is the most useful in L_3-L_3 grooming, as it is the power stroke, where the spurs' resistance to extension would be used. The upstroke is simply a return stroke. Although the spurs may be used to groom the ipsilateral wing (Farish 1972), we did not observe this behavior in cicada killers.

The utility of hind tibial spurs for L_3-L_3 grooming suggests that the spurs evolved from smaller setae, but it does not adequately explain their exaggerated size in female *Sphecius*. It seems unlikely that the grooming requirements of the female cicada killer would be so much greater than that of a male, or of other Hymenoptera, that such elaborate structures would evolve.

Howes (1919) suggests that the spurs of female *S. speciosus* are used to support the cicada during flight as "she squeezes [the spurs] against the cicada's sides and thus secures her burden during the overland journey to the burrow." When the spurs were removed from one wasp, the next cicada was carried in a more vertical position (Howes 1919). While Howes' (1919) single anecdotal observation weakly supports his suggestion that the spurs have a role in prey carriage, we do not believe the spurs can function in the manner suggested. The hind legs wrap around the cicada at high tibiotarsal angles (J.R. Coelho pers. obs.); therefore, the spurs would not be extended. If squeezed against the sides of the cicada, the spurs will lie flat against the tarsus, as they have almost no capacity to resist flexion.

In reviewing videotaped bouts of digging, we noted that although cicada killers are capable of buzzing to produce a powerful vibration (Coelho 1998), and many Hymenoptera use vibration to loosen soil (Spangler 1973), cicada killers did not buzz while digging. The compact soil was chewed from the walls of the burrow using the mandibles, and the fore legs were used in rapid motions to rake the loose particles below and behind the wasp. Hence, cicada killers are "rakers" in that they use the fore legs as rakes to move soil (Evans and West Eberhard 1970). Spines on the tarsus of the fore leg of *S. speciosus* form a pecten (rake), which is believed to augment the efficiency of raking (Evans 1966, Evans and West Eberhard 1970). Although raking moves the soil beyond the posterior margin of the animal, it does not necessarily clear it from the burrow or its entrance. As a unique type of "pusher," the female cicada killer uses the hind legs, as opposed to the abdomen, to move soil out of the burrow and beyond (Evans and West Eberhard 1970). She backs out of the burrow, thrusting each hind leg first posteriorly then laterally, removing soil from her path. The tibiotarsal angle appears to be low (near 90°) at the beginning of the motion when the leg is cocked, which extended the spurs. The path of the hind leg during the power stroke caused the spurs to be pushed against the soil in the direction of extension.

Hence, the high resistive force of the spurs is used to move additional dirt, thus increasing the efficacy of digging. Since little force is required for flexion, the spurs would not hinder the recovery stroke to complete the motion. This effect is similar to that of the "oars" of aquatic insects as they swim through the water (Gullan and Cranston 1994). When the spurs are fully extended, the effective surface area of the hind leg is substantially increased. Numerous setae on the tibia and tarsus probably also contribute to the effective surface area, which presumably allows the female to move more soil per stroke than she could otherwise, increasing the energetic efficiency of digging.

The resulting energy savings could be

used to dig more extensive burrows, to forage for additional cicadas, or for other fitness-enhancing activities. However, perhaps time is more limiting than energy. With an average lifespan of 13 days (Hastings 1989), they have little time to waste on burrow construction. Observations suggest that they carry out much of their digging at night (Dambach and Good 1943), which would avoid temporal conflicts with their strictly diurnal foraging bouts. Preliminary data from our laboratory (J.R. Coelho and A.J. Ross, pers. obs.) suggest that digging rates of cicada killers are consistent with completing a burrow in one night, as suggested by Dambach and Good (1943).

Hymenoptera tend to have long, thin, and even delicate legs, while a transport mechanism for soil should be large, broad, firm, and thick (Hildebrand 1985) as it is in mole crickets (*Gryllotalpa*), cicada nymphs (*Magicicada*) and certain scarab beetles (*Canthon*) (Gullan and Cranston, 1994). Evans (1966) states that the cicada killers' use of hind legs to move soil is "unusual among digger wasps," and Pate (1936) mentions the spurs as taxonomically important structural features of the genus *Sphecius*. The large hind tibial spurs of cicada killers appear to have been enhanced to function in digging while retaining their original function of grooming. Enlarged spurs appear to be an imperfect solution to the problem of fossorial adaptation in comparison to the highly derived morphology of fully fossorial insects. Nonetheless, cicada killers clearly are accomplished burrowers in addition to being excellent flyers. The spurs are lightweight and collapsible, which may make them a suitable compromise between the demands of different locomotory habits.

ACKNOWLEDGMENTS

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